THE UNIVERSITY of EDINBURGH

Edinburgh Research Explorer

Genetic parameters for resistance to nematode infections in Texel lambs and their utility in breeding programmes

Citation for published version:
Bishop, SC, Jackson, F, Coop, RL & Stear, MJ 2004, 'Genetic parameters for resistance to nematode infections in Texel lambs and their utility in breeding programmes', *Animal science*, vol. 78, pp. 185-194.

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Publisher's PDF, also known as Version of record

Published In:
Animal science

Publisher Rights Statement:
© 2004 British Society of Animal Science

General rights
Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.

Download date: 05. May. 2023

Animal Science 2004, **78:** 185-194 1357-7298 / 04 / 34340185$20·00
© 2004 British Society of Animal Science

Genetic parameters for resistance to nematode infections in Texel lambs and their utility in breeding programmes

S. C. Bishop[1]†, F. Jackson[2], R. L. Coop[2] and M. J. Stear[3]

[1]*Roslin Institute (Edinburgh), Roslin, Midlothian EH25 9PS, UK*
[2]*Moredun Research Institute, Penicuik, Midlothian EH26 9PZ, UK*
[3]*Department of Veterinary Clinical Studies, Glasgow University Veterinary School, Bearsden Road, Glasgow G61 1QH, UK*

† E-mail : stephen.bishop@bbsrc.ac.uk

Abstract

This paper addresses the inheritance of host resistance to gastro-intestinal nematode parasite infections in commercial Texel lambs, and the rôle of resistance to parasites in breeding programmes. In two flocks of Texel sheep, faecal egg counts following natural parasite challenge were measured on up to three occasions post weaning per lamb over a 4-year period, with 1385 and 287 lambs measured on the two farms. Live weight, and ultrasonically measured fat and muscle depth at weaning were available for each lamb, as were deep pedigrees. Egg counts were moderately to strongly heritable on all occasions, with Nematodirus *egg counts more heritable than the Strongyle egg counts. Weighted average heritabilities for Strongyle and* Nematodirus *egg counts were 0·26 and 0·38, respectively. Within the same category of parasite, genetic correlations across time were positive and strong but somewhat less than unity, as were the correlations between Strongyle and* Nematodirus *egg counts measured at the same time. Genetic correlations between performance traits and Strongyle egg counts were usually favourable (i.e. negative) but weak, whereas those with* Nematodirus *egg counts were generally neutral or slightly positive. Whilst* Nematodirus *resistance may not necessarily be included in a breeding goal, the results suggest that* Nematodirus *egg counts can be used as an additional genetic indicator of Strongyle egg counts, at little extra cost. Including the epidemiological consequences of decreasing Strongyle egg counts in benefits of increasing parasite resistance, it is suggested that under UK conditions selection goals that place equal emphasis on live weight and log-transformed egg counts will be a robust means of improving growth rate and decreasing parasite larval challenge.*

Keywords: *faecal egg counts, genetic parameters,* Nematodirus, *sheep,* Teladorsagia.

Introduction

Helminth infections constitute a major disease problem to domestic livestock worldwide (Perry *et al*., 2002), with most grazing livestock being at risk from infection by gastro-intestinal (GI) nematode parasites. Even in temperate sheep-producing regions, such infections can cause health and welfare problems. For example, ovine ostertagiosis (due to infection with the GI nematode *Teladorsagia circumcincta*) is a major constraint upon the productivity of growing lambs in the UK, with even sub-clinical infections causing marked decreases in productivity (Coop *et al*., 1982 and 1985). However, effective control of GI nematode parasites is becoming more difficult. The increasing problems of attaining effective parasite control through the use of anthelmintics due to the evolution of drug resistance in nematode parasite populations is well documented (e.g. Waller, 1997; Jackson and Coop, 2000), and this threatens sustainable sheep production throughout the world. The decreasing efficacy of anthelmintics coupled with the desire to move towards production systems less reliant upon chemical interventions has stimulated the search for alternative sustainable control measures.

The selection of sheep, particularly growing lambs, with enhanced resistance to GI nematode parasites is

often advocated as a control measure that may complement other strategies and, in the longer term, lead to a reduction in the requirements for anthelmintics. There is now considerable evidence for genetic variation amongst sheep in their resistance to GI nematode parasites. For example, variation between breeds is summarized by Gasbarre and Miller (2000), and the impact of this increased resistance in terms of overall efficiency of output is illustrated for the Red Maasai by Baker *et al*. (2002). Within-breed genetic variation in resistance to nematodes has been demonstrated in many countries and in many diverse host populations. Well known examples include the Merino (e.g. Woolaston and Piper, 1996; Woolaston and Windon, 2001), Romney (e.g. Morris *et al*., 1997 and 2000) and Scottish Blackface (Bishop *et al*., 1996; Stear *et al*., 1997), as well as feral Soay sheep (Smith *et al*., 1999). Furthermore, genetic variation in host resistance exists for the major nematode species affecting sheep: *Haemonchus contortus, Trichostrongylus colubriformis, T. circumcincta* and various *Nematodirus* species.

Many breeders within the terminal-sire sector of the UK sheep industry now wish to breed sheep with enhanced nematode resistance. However, several scientific and technical issues still require attention, foremost being the data upon which to base the breeding strategy and optimal weightings to be given to resistance vis-à-vis performance traits. Relevant field data are not available for terminal-sire breeds within the UK; at the time of the study, previously available data collected under UK conditions were obtained in a different breed, the Scottish Blackface, grazing in an environment unrepresentative of those normally encountered by terminal-sire breeds and their progeny, i.e. hill/upland instead of lowland. This paper seeks to fill the data gap by quantifying genetic variation in resistance to nematodes and genetic relationships with performance in two flocks of Texel sheep. Furthermore, the paper will explore issues relating to the incorporation of genetic information on resistance to nematodes into breeding programmes.

Material and methods

Animals and experimental design

Measurements were recorded on two flocks of Texel sheep. The first (flock 1) was a commercial flock producing approximately 400 lambs available for measurement every year and the second (flock 2) was a flock at Roslin Institute's Blythbank farm producing approximately 70 lambs every year.

Flock 1 participated in the Texel sire referencing scheme (Elite Texel Sires (UK) Ltd) and had pedigree data available from 1972. Additionally, performance data collected as part of the sire referencing scheme, i.e. live weight, ultrasonic muscle depth and ultrasonic fat depth at approximately 20 weeks of age, were available for all lambs in the flock since 1990. Flock 2 was created by upgrading a small flock of Texel-Oxford ewes as well as purchasing purebred Texel ewes. Sires used were all purebred Texel and were a mixture of rams donated by the Texel sire referencing scheme, purchased and homebred rams. Performance data collected included live weight, ultrasonic muscle depth and ultrasonic fat depth at approximately 20 weeks of age.

Parasitological data were collected on both farms over a period of four years from 1997 to 2000, following natural challenge. Faecal egg counts (FEC) were determined using a saturated salt flotation technique, modified from the method described by Christie and Jackson (1982). Eggs were classified according to whether they were Strongyle or *Nematodirus* spp. Strongyles are nematodes of the order Strongylida and in this particular case may include the following genera : *Oesophagostomum, Chabertia, Bunostomum, Trichostrongylus, Cooperia, Ostertagia, Teladorsagia* and *Haemonchus*. Previous results (Stear *et al*., 1998) suggest that on UK sheep farms the Strongyle populations will be dominated by *T. circumcincta*, with this species accounting for approximately three-quarters of all nematodes present in the GI tract of the sheep. The measurement technique, as implemented in this study, generally had a measurement increment of 1 egg per g (e.p.g.) from zero to 21 e.p.g., an increment of 3 e.p.g. from 21 to *ca*. 150 e.p.g., and an increment of 9 e.p.g. thereafter.

On farm 1, FECs were measured each year generally in early September when the lambs were approximately 6 months of age, and on either one or two other occasions, in July or in late October/early November. All sampling occasions were preceded 6 to 8 weeks earlier by anthelmintic treatment, generally with moxidectin (Cydectin, Fort Dodge Animal Health; a long-acting anthelmintic). Lambs were moved to fresh pasture following anthelmintic treatment. On farm 2, lambs were sampled on three occasions each year, in July, August and September, i.e. when the lambs were 5, 6 and 7 months of age, on average, in 1998-2000. In 1997, samples were collected in September, only. Each sample took place 4 weeks after anthelmintic treatment, either by ivermectin (Oramec drench, Merial Animal Health) or levamisole (Nilverm, Schering-Plough Animal Health), which were rotated between years. Lambs grazed the same pastures for the duration of the measurement period.

Table 1 *Summary statistics for Strongyle and* Nematodirus *faecal egg counts (FEC; eggs per g) on (a) farm 1 and (b) farm 2*

(a)	Strongyles			*Nematodirus*		
	July	September	November	July	September	November
No.	639	1385	447	639	1385	653
Arithmetic mean	126	166	248	74	107	44
Geometric mean	45	70	145	14	31	12
Proportion of zero values	0·11	0·05	0·01	0·20	0·13	0·22
Maximum†	982	1810	1819	910	2521	595
s. d.‡	1·67	1·52	1·14	1·52	1·69	1·75
(b)	Strongyles			*Nematodirus*		
	July	August	September	July	August	September
No.	212	217	287	212	217	287
Arithmetic mean	93	79	155	31	30	42
Geometric mean	17	22	41	5	5	6
Proportion of zero values	0·20	0·10	0·11	0·44	0·53	0·42
Maximum†	1647	806	1800	621	567	684
s. d.‡	1·52	1·67	1·56	1·45	1·40	1·76

† Shown is the largest individual observation.
‡ Shown is phenotypic standard deviation of ln(FEC + 1).

Data analysis

Data from the two farms were analysed separately as genetic links between the two farms were weak. Preliminary analyses of the data were performed using the GENSTAT package (Lawes Agricultural Trust, 1983) to determine significant fixed effects and test the distributional assumptions for the FECs. Significant fixed effects for both data sets and for most traits included year, sex, age of dam, rearing rank, age at measurement (which is confounded with day of birth) and the interaction of year with each of the other effects. Additionally on farm 2, genetic groups were fitted to account for whether base ewes were Texel-Oxford or purebred Texels, and whether founder sires were purchased or from the Texel sire referencing scheme. All FECs were positively skewed, and log-transformation was generally more effective in removing the skewness of the data than other transformations that were investigated, including the square- and cube-root transformations. The actual transformation used was ln(FEC + 1), with 1 being chosen as the factor added to FEC to avoid zero values because the measurement increment for low egg counts was 1.

Genetic parameters, and their standard errors, were estimated using the ASREML package (Gilmour *et al*., 1996), fitting an animal model including all known pedigree relationships between sheep. On farm 1 this consisted of 3890 animals, and on farm 2 1126 animals. In the univariate analysis of each trait, random effects fitted included direct genetic, between-year permanent environmental effect of the dam and a litter effect. The significance of including each additional random effect was tested using the likelihood ratio test. Bivariate analyses were performed using the most parsimonious model for each trait. Data were also analysed fitting a repeatability model, i.e. assuming that egg counts at different times on the same animal are repeated expressions of the same trait.

Results

Summary statistics for Strongyle and *Nematodirus* FEC are shown in Table 1a and b for farms 1 and 2, respectively. Egg counts are not strictly comparable across farms due to different sampling and management protocols, however they are broadly in agreement on the two farms, with Strongyle FECs being somewhat higher than *Nematodirus* FECs in both cases. Additionally, the relative variability of

Table 2 *Summary statistics for performance traits on farm 1 and 2*

	Farm 1			Farm 2		
	Weight (kg)	Muscle (mm)	Fat (mm)	Weight (kg)	Muscle (mm)	Fat (mm)
No.	2575	2575	2575	300	284	284
Mean	40·5	26·3	1·57	33·7	22·4	1·76
s.d.	4·47	2·66	0·66	5·22	2·57	0·42

Table 3 *Heritabilities* (h^2) *for Strongyle and* Nematodirus *faecal egg count on* (*a*) *farm 1 and* (*b*) *farm 2*

(a)	Strongyles			*Nematodirus*		
	July	September	November	July	September	November
h^2	0·25†	0·17	0·23	0·25	0·23	0·49
s.e.	0·10	0·05	0·12	0·10	0·06	0·11
(b)	Strongyles			*Nematodirus*		
	July	August	September	July	August	September
h^2	0·38	0·43	0·34	0·55	0·47	0·54
s.e.	0·17	0·17	0·15	0·16	0·18	0·14

† Common litter effect, as a proportion of the phenotypic variance, was 0·13 (s.e. 0·07).

Table 4 *Variance components for performance traits on farm 1 and 2*

	Farm 1			Farm 2		
	Weight	Muscle	Fat	Weight	Muscle	Fat
h^2	0·12	0·21	0·20	0·40	0·34	0·15
s.e.	0·04	0·05	0·05	0·21	0·21	0·14
m^2†	0·12	0·06	0·07	0·20	0·05	0·00
s.e.	0·03	0·02	0·02	0·10	0·08	0·07
c^2‡	0·19	0·12	0·09			
s.e.	0·13	0·03	0·03			

† Proportion of the phenotypic variance explained by between-year permanent environment effects attributable to the dam.
‡ Proportion of the phenotypic variance explained by common litter effects.

egg counts, as assessed by the phenotypic standard deviation of log-transformed FEC was similar for both genera and on both farms. Only for *Nematodirus* FECs on farm 2 were substantial numbers of zero counts observed. Performance traits are summarized in Table 2. In general, lambs were larger and less variable on farm 1.

Heritabilities for FEC are shown in Table 3a and b for farms 1 and 2, respectively. All values were moderate to high, with no discernable age trend. FEC was slightly but consistently more heritable on farm 2 than farm 1. Additionally, *Nematodirus* FECs were also consistently more heritable than Strongyle FECs. Permanent environment effects, i.e. dam and litter effects, tended to be small and not significant, apart from the July Strongyle FEC on farm 1, where the litter effect was significant. The weighted average heritability for Strongyle FECs across the whole dataset was 0·26, and for *Nematodirus* FEC it was 0·38.

Heritabilities and permanent environmental effects for performance traits are shown in Table 4. Unlike the FEC traits, permanent environmental effects tended to be significant for the performance traits, especially on farm 1 where both (across-year) maternal and litter effects were significant. Fitting the across-year maternal effect as a maternal genetic effect gave almost identical results for each trait, indicating that this effect is most probably genetic in origin. On farm 2, all litter effects were zero.

Phenotypic and genetic correlations between Strongyle and *Nematodirus* FECs measured at the same time are shown in Table 5. The genetic correlations between the genera are moderate to strong, but generally somewhat less than unity. The weighted average genetic correlation on farm 1 is 0·49 and on farm 2 is 0·71. The indication is that resistance to the two genera of parasites, as assessed by egg counts, is strongly correlated but not entirely

Table 5 *Phenotypic* (rp) *and genetic* (rg) *correlations between Strongyle and* Nematodirus *faecal egg counts*

	Farm 1			Farm 2		
	July	September	November	July	August	September
rp	0·20	0·32	0·38	0·36	0·46	0·41
rg	0·62	0·47	0·38	0·95	0·58	0·66
s.e.	0·24	0·18	0·25	0·32	0·25	0·22

Table 6 *Phenotypic* (rp) *and genetic* (rg) *correlations across time between faecal egg counts on* (*a*) *farm 1 and* (*b*) *farm 2*

(a)	July, September		July, November		September, November	
	Strongyles	*Nematodirus*	Strongyles	*Nematodirus*	Strongyles	*Nematodirus*
rp	0·32	0·34	0·25	0·18	0·31	0·46
rg	0·82	0·67	0·78	0·48	0·97	1·00
s.e.	0·15	0·15	0·22	0·25	0·14	0·09
(b)	July, August		July, September		August, September	
	Strongyles	*Nematodirus*	Strongyles	*Nematodirus*	Strongyles	*Nematodirus*
rp	0·38	0·60	0·43	0·52	0·52	0·61
rg	0·30	0·97	0·62	0·94	0·62	0·95
s.e.	0·32	0·14	0·27	0·15	0·26	0·10

the same phenomenon. Phenotypic correlations are stronger on farm 2 than on farm 1.

Phenotypic and genetic correlations between FECs from the same genera, but measured at different times are shown in Table 6a and b for farms 1 and 2, respectively. Phenotypic correlations across time are stronger on farm 2 than farm 1. Genetic correlations across time tend to be moderate to strong, indicating that resistance at different ages is largely, but not entirely the same trait, i.e. the genetic control of resistance is evolving with time.

Correlations between FEC and performance traits are shown in Table 7a and b for farms 1 and 2, respectively. The dataset on farm 2 was insufficient to provide meaningful genetic correlations with fat depth. Most phenotypic correlations between performance and parasitological traits are close to zero. Genetic correlations tend to be variable, and have large standard errors due to the small dataset on farm 2 and the generally lower heritabilities seen on farm 1. The main observable trend is that correlations with *Nematodirus* FEC are almost always more positive than those with Strongyle FEC. Taking weighted averages of the correlations across time adds clarity. On farm 1, the average genetic correlations between live weight and Strongyle and *Nematodirus* FEC are –0·20 and 0·13, respectively. For muscle depth these correlations are 0·10 and 0·18,

Table 7 *Phenotypic* (rp) *and genetic* (rg) *correlations between faecal egg counts and performance traits on* (*a*) *farm 1 and* (*b*) *farm 2*

(a)		Strongyles			*Nematodirus*		
		July	September	November	July	September	November
Weight	*rp*	–0·03	–0·05	–0·03	0·07	–0·03	–0·05
	rg	–0·02	–0·12	–0·47	0·26	0·21	–0·07
	s.e.	0·28	0·25	0·28	0·27	0·22	0·22
Muscle	*rp*	–0·05	–0·03	–0·08	0·04	0·02	–0·01
	rg	0·05	0·43	–0·38	0·08	0·31	0·12
	s.e.	0·21	0·17	0·29	0·24	0·17	0·19
Fat	*rp*	–0·17	–0·05	–0·07	0·03	–0·02	–0·08
	rg	–0·14	0·13	–0·23	0·00	0·05	–0·08
	s.e.	0·24	0·22	0·29	0·26	0·19	0·20
(b)		Strongyles			*Nematodirus*		
		July	August	September	July	August	September
Weight	*rp*	–0·11	0·01	–0·02	–0·02	0·00	–0·03
	rg	–0·36	–0·02	0·18	0·16	0·34	0·18
	s.e.	0·34	0·35	0·29	0·33	0·32	0·28
Muscle	*rp*	–0·17	–0·02	0·02	0·00	–0·08	–0·04
	rg	–0·38	–0·51	0·06	0·30	0·16	0·28
	s.e.	0·32	0·30	0·33	0·28	0·32	0·25

Table 8 *Variance components for faecal egg count, using a repeatability model*

	Farm 1		Farm 2	
	Strongyles	*Nematodirus*	Strongyles	*Nematodirus*
h^2	0·20	0·26	0·24	0·45
s.e.	0·04	0·05	0·10	0·11
repeatability	0·28	0·38	0·45	0·57
s.e.	0·03	0·03	0·04	0·04

and for fat depth they are –0·06 and –0·01. On farm 2, the average genetic correlations between live weight and Strongyle and *Nematodirus* FEC are –0·05 and 0·23, and for muscle depth they are –0·29 and 0·25, respectively. When averaged across the whole data set, the genetic correlation between live weight and FEC was –0·13 for Strongyles and 0·17 for *Nematodirus*. Likewise, the genetic correlation between muscle depth and FEC was –0·05 for Strongyles and 0·21 for *Nematodirus*.

Variance components from the repeatability analyses are shown in Table 8. The heritabilities were lower than the weighted average heritabilities from the equivalent univariate analyses, in agreement with the observation that the across-time genetic correlations are less than unity, i.e. the trait is changing over time. Correlations with performance traits from the repeatability analyses are shown in Table 9 for farm 1. Data from farm 2 was insufficient for these analyses to converge. These correlations are generally similar to or marginally more negative (favourable) than those obtained by averaging the univariate analyses, adding confidence to our results.

Table 9 *Genetic correlations between faecal egg count and performance traits on farm 1, using a repeatability model*

Trait		Strongyles	*Nematodirus*
Live weight	Correlation	–0·19	–0·09
	s.e.	0·14	0·11
Muscle depth	Correlation	–0·11	0·05
	s.e.	0·12	0·11
Fat depth	Correlation	–0·19	–0·09
	s.e.	0·12	0·11

Discussion

Experimental findings and implications

We have explored genetic variation in nematode resistance in Texel lambs grazing pasture conditions typical of those seen under UK conditions. Our main results may be summarized as follows. Lambs on these two farms were consistently infected by nematode parasites, both Strongyles and, to a lesser extent, *Nematodirus* spp. This was despite regular anthelmintic treatment and, on farm 1, regular movement of lambs between pastures. It should be noted that Strongyle egg counts from infections dominated by *T. circumcincta* are typically considerably lower than those from infections dominated by *T. colubriformis* or *H. contortus*. The distribution of egg counts followed the typically skewed distribution seen with nematode infections, and the phenotypic standard deviation of log-transformed counts was generally slightly greater than the rule-of-thumb value of 1·0. This was due to the transformed data sometimes, but not always, being slightly left-skewed. When egg counts were transformed by ln(FEC + 9), where 9 is the measurement increment for high egg counts, the phenotypic standard deviations were invariably close to 1·0.

On all occasions between-animal variation in egg counts was heritable, and on every occasion *Nematodirus* egg counts were more heritable than Strongyle egg counts. Heritabilities were also considerably higher on farm 2 than on farm 1, however this was consistent for performance traits as well as egg count traits and presumably is at least

Table 10 *Predicted responses to selection from selection indices using consensus genetic parameters and differing relative economic values for egg counts, and the relative improvement in total live-weight gain from measuring egg counts*

	Egg counts not measured			Egg counts measured			
r.e.v.†	ΔWeight direct (kg)	Δ(ln (egg counts))	ΔWeight total (kg)	ΔWeight direct (kg)	Δln (egg counts))	ΔWeight total (kg)	Relative improvement
0	1·125	–0·05	1·125	1·150	–0·091	1·150	1·022
–0·5	1·125	–0·05	1·238	1·058	–0·184	1·473	1·190
–1·0	1·125	–0·05	1·350	0·924	–0·226	1·940	1·437
–1·5	1·125	–0·05	1·463	0·820	–0·245	2·472	1·690
–2·0	1·125	–0·05	1·575	0·746	–0·254	3·034	1·927

† r.e.v. is the relative economic value for log-transformed egg counts, calculated as δ(live weight)/δ(ln(egg count)).

partly attributable to selection history of the two flocks. For example, the flock on farm 2 was upgraded from a flock of Texel-Oxford ewes and it has used rams from a wide variety of sources which, despite the fitting of genetic groups, may have increased the genetic variation in the flock. In contrast, the flock on farm 1 was a pedigree-recorded flock in which rams were selected on the industry-standard lean growth index (Simm and Dingwall, 1989). The heritabilities were robust to the transformation used. For example, for transformations of ln(FEC + 1), ln(FEC + 9) and ln(FEC + 25) the estimated heritabilities seldom differed by more than ±0·02 and no consistent trend was apparent. Egg counts were always positively correlated across time and positively correlated between parasite genera, although both phenotypic and genetic correlations were usually less than unity. The fact that the genetic correlations across time were usually less than unity may be interpreted in terms of the developing immune response with age and exposure. Likewise, the possibility that some but not all resistance mechanisms are shared for different genera of parasites accounts for the medium to strong correlations between genera.

Lastly, genetic correlations between performance traits and egg counts were not consistent across time or across farms. When correlations are averaged across time or estimated using a repeatability model, correlations of performance traits with Strongyle egg counts tend to be slightly negative, i.e. favourable, and those with *Nematodirus* egg counts tend to be neutral or slightly positive, i.e. unfavourable.

The heritabilities of Strongyle egg counts are in broad agreement with most previously published values obtained under temperate conditions, for both natural challenge (e.g. Bishop *et al*., 1996; Eady *et al*., 1996; Bouix *et al*., 1998; McEwan *et al*., 1992 and 1995) and artificial challenge (e.g. Sreter *et al*., 1994; Gruner and Lantier, 1995; Woolaston and Piper, 1996; Woolaston and Windon, 2001). As a summary, heritabilities for Strongyle egg counts are usually in the range 0·2 to 0·4, i.e. similar to most performance traits in lambs, however egg counts are generally considerably more variable than performance traits, giving considerable opportunities for genetic progress if they are used as a measured trait in a breeding programme.

In contrast to the now adequate literature on Strongyle egg counts there are few published genetic parameters for *Nematodirus* egg counts, although McEwan *et al*. (1992 and 1995) report values respectively slightly higher than and similar to corresponding values for Strongyle egg counts. Additionally heritabilities for *Nematodirus* egg counts obtained on Scottish Blackface lambs ranged between 0·20 and 0·35 (S. C. Bishop and M. J. Stear, unpublished results), and were greater than corresponding heritabilities for Strongyle egg counts on every sampling occasion.

The pathogenic effects of autumn *Nematodirus* infections are not well documented, and there is currently little justification for incorporating them into a breeding goal. However, the fact that they are genetically correlated with Strongyle egg counts and, in our environment, more strongly heritable than Strongyle egg counts suggests that they can be used as an indicator trait. For example, assuming weighted average heritabilities of 0·25 and 0·35, respectively for Strongyle and *Nematodirus* egg counts, and genetic and phenotypic correlations between the two traits of 0·60 and 0·35, respectively, then including *Nematodirus* egg counts as an indicator trait allows an additional 7% genetic progress, at essentially no extra cost. This assumes that log-transformed *Nematodirus* egg counts are normally distributed and that the majority of lambs have non-zero FEC values, as was seen on most occasions in our data. Additionally, and perhaps more importantly, they provide an insurance mechanism should the Strongyle challenge be insufficient or too inconsistent to produce meaningful egg counts. This scenario has been observed in separate studies on other sheep (S. C. Bishop and M. J. Stear, unpublished).

Considerable variability exists in published relationships between Strongyle egg counts and lamb growth traits. Hitherto, published values from European studies have tended to be negative and strong, e.g. –0·8 between egg counts and live weight in Scottish Blackface lambs (Bishop *et al*., 1996) and –0·6 for the same traits in Polish lambs (Bouix *et al*., 1998). Under New Zealand and Australian conditions, such strong correlations are seldom seen, with values generally being between 0 and –0·3 (e.g. Bisset *et al*., 1992; Douch *et al*., 1995; Eady *et al*., 1998), however slightly positive correlations have also been reported (e.g. McEwan *et al*., 1992 and 1995). The values reported here, although variable, tend towards the consensus mean values, i.e. slightly negative. Correlations of *Nematodirus* egg counts with lamb growth are not well documented, although McEwan *et al*. (1992) reports genetic correlations that are more negative than the corresponding correlations with Strongyle egg counts. This result is the opposite of what we observed.

Interpretation of resistance in a breeding context

Consensus parameter values for egg counts may easily be put into selection indices, however they do not address the issue of the relative importance of resistance, i.e. the weighting that should be given to this trait. Including GI parasite resistance in breeding goals may benefit sheep production enterprises in a number of ways, for example (i) direct increases in productivity resulting from favourable genetic correlations between resistance and performance, (ii) decreased pasture contamination, leading indirectly to improved performance, (iii) decreased treatment costs and (iv) less tangible benefits such as improved health and welfare. The genetic correlation between resistance and performance will influence the nature of the benefits of improving resistance. As the correlation becomes progressively less favourable, the benefits will change from direct improvements in productivity to less easily quantifiable benefits via decreased pasture contamination, improved health and welfare, and decreased treatment costs. The relatively weak correlations observed in this study suggest that benefits from improving the resistance of Texel sheep will be of the latter type.

Epidemiological benefits of improving the resistance of sheep to parasites, by means of decreased pasture contamination, have been postulated and quantified *in silico* by a number of authors, including Barger (1989) and Bishop and Stear (1997 and 1999). However, recent experimental evidence has verified these computer-based predictions. For example, Leathwick *et al*. (2002) reported a trial in which lines of sheep previously selected for high and low egg counts grazed separate replicated fields, allowing epidemiological effects resulting from decreased pasture contamination to accumulate across the grazing season, over a period of three years. Large differences in egg counts and pasture contamination were observed and, importantly, previous line differences of 1·7 kg lamb live weight and 5% and 8% fleece weight in lambs and ewes, respectively, which arose from unfavourable genetic correlations between performance and resistance in these New Zealand populations, disappeared. Likewise, Gruner *et al*. (2002) created epidemiological differences by grazing separate fields with sheep selected for either high or low egg counts, then monitored the consequences using unselected tracer lambs. Pasture larval contamination differed substantially between the two treatments and tracer lambs on the fields grazed by 'resistant' sheep had substantially lower worm burdens, especially for *T. circumcincta* and *H. contortus*, than those on fields grazed by 'susceptible' sheep The implication of these two studies is that selection for resistance may lead to large differences in pasture contamination, with consequent changes in parasite burden and performance.

These epidemiological consequences of selection lead to a simple means of quantifying the benefits of selection and hence exploring the relative weighting that should be given to resistance. Bishop and Stear (1999) modelled the consequences of reducing Strongyle egg counts, and hence pasture larval contamination, and predicted that lamb live weight would increase as a result, in agreement with the experimental findings described above. Thus, live weight may be used as the common currency, with the economic weight for egg counts being the change in live weight per unit change in flock average egg count. The aggregate genotype for an individual (T) is then $\mathbf{Y'v}$, where $\mathbf{Y}$ is a vector of estimated breeding values for live weight and Strongyle egg counts, and $\mathbf{v}$ is a vector of relative economic weights for these two traits, i.e. $\mathbf{v'}$ comprises values [1, δ(live weight)/ δ(ln(egg count))]. The direct live-weight component of the aggregate genotype will be expressed by each animal, however the component arising from the egg count genotype will only be expressed at the flock level, i.e. as the average of the individual breeding values.

The quantity δ(live weight)/ δ(ln(egg count)) may be estimated from the results presented by Bishop and Stear (1999). Using their year 1 results and subtracting changes in live weight arising as a genetically correlated response from altering egg counts, then Δ(live weight) / Δ(ln(egg count) is estimated to be –1·28, i.e. close to –1·0. Using the more general value of –1, the consequences of including egg counts in a selection index may be calculated using genetic parameters taken directly from this study, *viz*. heritability for live weight and Strongyle egg counts of 0·25, and 0·35 for *Nematodirus* egg counts; genetic and phenotypic correlations of 0·6 and 0·35 between Strongyle and *Nematodirus* egg counts, –0·2 and 0·0 between live weight and Strongyle egg counts and 0·0 and 0·0 between live weight and *Nematodirus* egg counts. Lastly, the phenotypic standard deviation for live weight was assumed to be 4·5 kg. Indicative responses to selection for a single round of selection with one standardized unit of selection intensity are shown in Table 10. It should be noted that even when egg counts are not measured, an economic weighting for egg counts indicates that correlated responses in this trait will contribute to the overall gain in live weight of the flock as a whole.

The results presented in Table 10 show that including Strongyle and *Nematodirus* egg count measurements, and applying an economic weight to Strongyle egg

counts, results in a substantial predicted increase in flock live weight. However this total gain is achieved to some extent at the expense of direct responses in live weight. For example, for a relative economic weight of –1·0, total live-weight gain is improved by a factor of 1·44, although direct responses are reduced to 0·82 of what they would have been without selection on egg counts. Nevertheless, for a wide range of relative economic values for egg counts substantial direct progress in live weight is achieved and the extra benefits from decreasing pasture contamination may be substantial. It must be appreciated that these results are specific to data, models and genetic parameters relevant to grazing conditions and parasite species typical of the UK. The principles may be extrapolated to other production circumstances, however the methodology would have to be validated with data relevant to those conditions, and the results obtained may well differ.

The results presented here are based on the assumption that treatment protocols remain unchanged. Selection indices in which benefits come partly from reduced anthelmintic requirements were explored by Woolaston (1994). Although the nature of the calculations differ from our study, the overall conclusion is the same insofar as including egg counts in the objective can lead to substantial gains in the overall breeding goal, and this remains true for a wide range of emphasis placed on egg counts. A more formal, albeit considerably more complex, estimate of economic values for parasite resistance was presented by Amer *et al*. (1999), accounting for production losses and epidemiological effects, but leaving treatment costs unchanged. As may be expected, the economic weights varied according to the production system, but rescaling results of Amer *et al*. (1999) and considering lamb growth rate alone, relative values similar to the 1 : -1 suggested in this paper are obtained. Thus, independent studies indicate considerable value from improving resistance, and these benefits may be obtained without sacrificing much direct gain in live weight.

Conclusions

This paper has demonstrated that it is feasible, in principle, to select sheep for resistance to gastrointestinal nematode parasites under typical commercial sheep conditions in the UK where sheep face a natural parasite challenge. Extra benefit will be obtained from basing selection on both Strongyle and *Nematodirus* egg counts. Some benefit is predicted to come directly due to a moderate but favourable genetic correlation between live weight and Strongyle egg counts, however greater benefit is predicted from the indirect benefits of reducing pasture larval contamination. Selection index calculations suggest that considerable extra gains are achievable for a wide range of relative economic weightings given to egg counts.

Acknowledgements

We thank the Meat and Livestock Commission and the Scottish Executive Environment and Rural Affairs Department for funding this project through LINK Sustainable Livestock Production. The input from Elite Texel Sires (UK) Ltd, especially Richard Oates and the late Peter Johnson, is gratefully appreciated. We thank the staff at Blythbank and Lumbylaw farms for their efforts and inputs.

References

Amer, P. R., Woolaston, R. R., Eady, S. J. and McEwan, J. C. 1999. Economic values for sheep internal parasite resistance traits in New Zealand and Australia. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **13:** 504-507.

Baker, R. L., Mugambi, J. M., Audho, J. O., Carles, A. B. and Thorpe, W. 2002. Comparison of Red Maasai and Dorper sheep for resistance to gastro-intestinal nematode parasites, productivity and efficiency in a sub-humid and a semi-arid environment in Kenya. *Proceedings of the seventh world congress on genetics applied to livestock production, Montpellier,* communication 13-10.

Barger, I. A. 1989. Genetic resistance of hosts and its influence on epidemiology. *Veterinary Parasitology* **32:** 21-35.

Bishop, S. C., Bairden, K., McKellar, Q. A., Park, M. and Stear, M. J. 1996. Genetic parameters for faecal egg count following mixed, natural, predominantly *Ostertagia circumcincta* infection and relationships with live weight in young lambs. *Animal Science* **63:** 423-428.

Bishop, S. C. and Stear, M. J. 1997. Modelling responses to selection for resistance to gastro-intestinal parasites in sheep. *Animal Science* **64:** 469-478.

Bishop, S. C. and Stear, M. J. 1999. Genetic and epidemiological relationships between productivity and disease resistance: gastro-intestinal parasite infection in growing lambs. *Animal Science* **69:** 515-524.

Bisset, S. A., Vlassof, A., Morris, C. A., Southey, B. R., Baker, R. L. and Parker, A. G. H. 1992. Heritability of and genetic correlations among faecal egg counts and productivity traits in Romney sheep. *New Zealand Journal of Agricultural Research* **35:** 51-58.

Bouix, J., Krupinski, J., Rzepecki, R., Nowosad, B., Skrzyzala, I., Roborzynski, M., Fudalewicz-Niemczyk, W., Skalska, M., Malczewski, A. and Gruner, L. 1998. Genetic resistance to gastrointestinal nematode parasites in Polish long-wool sheep. *International Journal for Parasitology* **28:** 1797-1804.

Christie, M. G. and Jackson, F. 1982. Specific identification of strongyle eggs in small samples of sheep faeces. *Research in Veterinary Science* **32:** 113-117.

Coop, R. L., Graham, R. B., Jackson, F., Wright, S.E. and Angus, K. W. 1985. Effect of experimental *Ostertagia circumcincta* infection on the performance of grazing lambs. *Research in Veterinary Science* **38:** 282-287.

Coop, R. L., Sykes, A. R. and Angus, K. W. 1982. The effect of three levels of *Ostertagia circumcincta* larvae on growth rate, food intake and body composition of growing lambs. *Journal of Agricultural Science, Cambridge* **98:** 247-255.

Douch, P. G. C., Green, R. S., Morris, C. A., Bisset, S. A., Vlassoff, A., Baker, R. L., Watson, T. G., Hurford, A. P. and Wheeler, M. 1995. Genetic and phenotypic relationships among anti-*Trichostrongylus colubriformis* antibody level, faecal egg count and body weight traits in grazing Romney sheep. *Livestock Production Science* **41:** 121-132 .

Eady, S. J., Woolaston, R. R., Lewer, R. R., Raadsma, H. W., Swan, A. A. and Ponzoni, R. W. 1998. Resistance to gastrointestinal parasites in Merino sheep: correlation with production traits. *Australian Journal of Agricultural Research* **49:** 1201-1211.

Eady, S. J., Woolaston, R. R., Mortimer, S. I., Lewer, R. P., Raadsma, H. W., Swan, A. A. and Ponzoni, R. W. 1996. Resistance to nematode parasites in Merino sheep: sources of genetic variation. *Australian Journal of Agricultural Research* **47:** 895-915.

Gasbarre, L. C. and Miller, J. E. 2000. Genetics of helminth resistance. In *Breeding for disease resistance in farm animals, second edition* (ed. R. F. E. Axford, S. C. Bishop, F. W. Nicholas and J. B. Owen), pp. 129-152. CABI Publishing, Wallingford.

Gilmour, A. R., Thompson, R., Cullis, B. R. and Welham, S. 1996. *ASREML*. Biometrics bulletin no. 3, NSW Agriculture.

Gruner, L., Cortet, J., Sauve, C., Limouzin, C. and Brunel, J. C. 2002. Evolution of nematode community in grazing sheep selected for resistance and susceptibility to *Teladorsagia circumcincta* and *Trichostrongylus colubriformis*: a 4-year experiment. *Veterinary Parasitology* **109:** 277-291.

Gruner, L. and Lantier, F. 1995. Breeding for resistance to infectious diseases in small ruminants in Europe. In *Breeding for resistance to infectious diseases in small ruminants* (ed G. D. Gray, R. R. Woolaston and B. T. Eaton). ACIAR, Canberra.

Jackson, F. and Coop, R. L. 2000. The development of anthelmintic resistance in sheep nematodes. *Parasitology* **120:** S95-S107.

Lawes Agricultural Trust. 1983. *GENSTAT a general statistical program*. Numerical Algorithms Group, Rothamsted Experimental Station, Harpenden.

Leathwick, D. M., Atkinson, D. S., Miller, C. M., Brown, A. E. and Sutherland, I. A. 2002. Benefits of reduced larval challenge through breeding for low faecal egg count in sheep. Novel approaches. III. *A workshop meeting on helminth control in livestock in the new millennium, Moredun Research Institute, 2-5 July, 2002*, p. 10.

McEwan, J. C., Dodds, K. G., Greer, G. J., Bain, W. E., Duncan, S. J., Wheeler, R., Knowler, K. J., Reid, P. J., Green, R. S. and Douch, P. G. C. 1995. Genetic estimates for parasite resistance traits in sheep and their correlations with production traits. *New Zealand Journal of Zoology* **22:** 177.

McEwan, J. C., Mason, P., Baker, R. L., Clarke, J. N., Hickey, S. M. and Turner, K. 1992. Effect of selection for productive traits on internal parasite resistance in sheep. *Proceedings of the New Zealand Society of Animal Production* **52:** 53-56.

Morris, C. A., Vlassoff, A., Bisset, S. A., Baker, R. L., Watson, T. G., West, C. J. and Wheeler, M. 2000. Continued selection of Romney sheep for resistance or susceptibility to nematode infection: estimates of direct and correlated responses. *Animal Science* **70:** 17-27.

Morris, C. A., Vlassof, A., Bisset, S. A., Baker, R. L., West, C. J. and Hurford, A. P. 1997. Responses of Romney sheep to selection for resistance or susceptibility to nematode infection. *Animal Science* **64:** 319-329.

Perry, B. D., McDermott, J. J., Randolph, T. F., Sones, K. R. and Thornton, P. K. 2002. *Investing in animal health research to alleviate poverty.* International Livestock Research Institute, Nairobi, Kenya.

Simm, G. and Dingwall, W. S. 1989. Selection indices for lean meat production in sheep. *Livestock Production Science* **21:** 223-233.

Smith, J. A., Wilson, K., Pilkington, J. G. and Pemberton, J. M. 1999. Heritable variation in resistance to gastro-intestinal nematodes in an unmanaged mammal population. *Proceedings of the Royal Society of London, Series B-Biological Sciences* **266:** 1283-1290.

Sreter, T., Kasaai, T. and Takacs, E. 1994. The heritability and specificity of responsiveness to infections with *Haemonchus contortus* in sheep. *International Journal for Parasitology* **24:** 871-876.

Stear, M. J., Bairden, K., Bishop, S. C., Gettinby, G., McKellar, Q. A., Park, M., Strain, S. and Wallace, D. S. 1998. The processes influencing the distribution of parasitic nematodes amongst naturally infected lambs. *Parasitology* **117:** 165-171.

Stear, M. J., Bishop, S. C., Bairden, K., Duncan, J. L., Gettinby, G., Holmes, P. H., McKellar, Q. A., Park, M., Strain, S. and Murray, M. 1997. The heritability of worm burden and worm fecundity in lambs following natural nematode infection. *Nature* **389:** 27.

Waller, P. J. 1997. Anthelmintic resistance. *Veterinary Parasitology* **72:** 391-405.

Woolaston, R. R. 1994. Preliminary evaluation of strategies to breed Merinos for resistance to roundworms. *Proceedings of the fifth world congress on genetics applied to livestock production, Guelph, vol. 20*, pp. 281-284.

Woolaston, R. R. and Piper, L. R. 1996. Selection of Merino sheep for resistance to *Haemonchus contortus*: genetic variation. *Animal Science* **62:** 451-460.

Woolaston, R. R. and Windon, R. G. 2001. Selection of sheep for response to *Trichostrongylus colubriformis* larvae: genetic parameters. *Animal Science* **73:** 41-48.

(*Received* 31 *March* 2003—*Accepted* 20 *September* 2003)